1   **Title:** Ecological memory mitigates negative impacts of disturbance on biomass production in

2   benthic diatom metacommunities

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18   **Abstract**

19   Disturbance events to coastal habitats such as extreme heat events, storms, or floods

20   have increased in magnitude and frequency in recent years due to anthropogenic climate

21   change and the destruction of habitats. These events constitute a major threat to many

22   ecological communities and global biodiversity. Disturbance history influences ecosystem

23   response to novel disturbances such that communities that have previously been exposed to

24   disturbances should be more resilient to new disturbances compared to previously sheltered

25   communities. This principle is defined as ecological memory. Resilience should also increase

26   with access to a larger species pool, because a larger species pool increases species and

27   response diversity of a community. One possibility of increasing the local species pool is

28   connectivity via adequate dispersal between habitat patches with different species

29   compositions in metacommunities. In a laboratory experiment, we exposed benthic diatom

30   communities of different origin to a mechanical disturbance, simulated dispersal in half of the

31   communities, and measured their chlorophyll *a* concentration over time. The local diatom

32   communities originated from different locations on an intertidal flat that varied in

33   hydrodynamic exposure history. Hydrodynamic exposure disturbs the sediment, and thereby

34   determines sediment properties and the composition of intertidal diatom communities. In the

35   experiment, disturbance negatively affected chlorophyll *a* concentration across all treatments.

36   However, the response to disturbance depended on the ecological memory of the

37   communities; the more exposed areas the communities originated from, the less negative was

38   the effect of the mechanical disturbance. Interestingly, dispersal did not mitigate the negative

39   impacts of disturbance in any of the communities. Our results highlight the importance of

40   ecological memory for ecosystem functioning and demonstrate the limitations of patch

41   connectivity to alleviate the impacts of disturbance events in metacommunities.

42   **Keywords:** dispersal; resilience; microalgae; origin; species composition

43   **Introduction**

44   Global climate change and habitat destruction have altered many ecosystems which poses

45   an urgent threat to many ecological communities and thus to global biodiversity (IPCC 2014).

46   In addition to increased average global temperatures, the severity and frequency of extreme

47   weather events such as storms and floods are expected to increase in the future (Harley et al.

48   2006, IPCC 2014). These extreme events will severely affect coastal areas, including the

49   North Sea coast (Beniston et al. 2007), where they disturb and redistribute surface sediments

50   on intertidal flats (Bartholomä et al. 2009). Increased sediment dynamics caused by storms

51   and floods will most likely affect intertidal production negatively, because sediment erosion is

52   the main abiotic constraint for autotrophic organisms living in and on surface sediments (de

53   Jonge and van Beusekom 1995, Donadi et al. 2013a). Resilience in the face of disturbances is

54   crucial for the survival of ecological communities and the maintenance of ecological

55   functions in our fast-changing world (Oliver et al. 2015, König et al. 2019).

56   Species diversity affects ecosystem functioning (Hooper et al. 2005, Cardinale et al. 2012,

57   Gonzalez et al. 2020) and influences ecosystem responses to disturbances by determining the

58   system's response diversity and resilience (Elmqvist et al. 2003, Mori et al. 2013). Higher

59   response diversity increases the resilience of communities and thus assures the maintenance

60   of ecosystem functioning during and after disturbance events (Elmqvist et al. 2003, Mori et al.

61   2013, Carrara et al. 2015, Oliver et al. 2015). Species and response diversity are increased in

62   communities with access to a larger, regional species pool, compared to local isolated

63   communities, if the different local communities have varying species compositions (Altermatt

64   et al. 2011, Cosentino et al. 2011). Individual local communities that are connected via

65   dispersal (i.e. the passive or active movement of individuals from one local patch to another)

66   form metacommunities (Gilpin and Hanski 1991, Wilson 1992, Leibold et al. 2004, Holyoak

67   et al. 2005). Increased species and response diversity in metacommunities are mainly caused

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68   by the sampling effect (Loreau and Hector 2001) and the spatial insurance effect (Loreau et

69   al. 2003, Leibold and Chase 2018). Both these principles are based in the theory that access to

70   a regional species pool with diverse traits increases the probability of local patch colonization

71   by superior species that can maximize ecosystem functioning. In addition, mass effects

72   (Mouquet and Loreau 2003) that lead to the constant replenishment of biomass from the

73   regional species pool, and thus supply regional dominant species to local patches, can aid in

74   the resilience of communities.

75   Previous states and experiences can affect future responses of communities, a process

76   coined as "ecological memory" (Padisak 1992, Ogle et al. 2015). Ecological memory can

77   manifest in different ways including the retention of certain physiological, behavioral,

78   morphological, molecular, or ecological attributes that were shaped by previous exposure to

79   specific conditions (Schweiger et al. 2019). These retained attributes can greatly affect how

80   communities cope with novel disturbances such that communities that previously experienced

81   disturbances are often more resilient towards novel disturbances (Bengtsson et al. 2003,

82   Johnstone et al. 2016, Hughes et al. 2019). In this study, we focus on an ecological,

83   community-level component of ecological memory, i.e. how species composition, which was

84   shaped by past experiences, influences the response of the community to a novel disturbance.

85   Coastal areas are among the most productive ecosystems on the planet and have great

86   ecological and economic value (Heip et al. 1995, Harley et al. 2006). Intertidal mudflats

87   harbor a multitude of different species from all domains of life. Microalgae are the main

88   primary producers fueling these diverse benthic food webs (Markert et al. 2013, Rigolet et al.

89   2014). Benthic microalgae contribute up to 50% of total primary production in some intertidal

90   areas where they can form extensive biofilms on surface sediments (Underwood and

91   Kromkamp 1999, Decho 2000, Stal 2003, Kromkamp et al. 2006). Benthic microalgae

92   biomass and diversity is regulated by many different factors, among them resource

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93   availability and grazing (Underwood and Kromkamp 1999, Weerman et al. 2011a, 2011b).

94   The presence of ecosystem engineers such as mussels or oysters also greatly influences

95   benthic microalgae biomass and species composition (Donadi et al. 2013a, Engel et al. 2017).

96   By creating solid structures on intertidal flats, mussel and oyster beds create clear gradients in

97   hydrodynamic conditions and sediment properties (e.g. sediment grain size and organic matter

98   content), which affect species composition and biomass of many organisms including benthic

99   diatoms (Widdows and Brinsley 2002, Donadi et al. 2013b, van der Zee et al. 2012).

100   In a microcosm experiment with intertidal benthic diatoms, we tested the importance of

101   ecological memory and access to a regional species pool for the community's resilience to

102   recurring disturbance events. The diatom communities originated from sites with different

103   histories of hydrodynamic stress. We exposed the diatom communities to mechanical

104   disturbance (physical destruction of biofilm), simulated dispersal between the communities

105   with different origin, and measured their chlorophyll *a* concentration (i.e. biomass) over time.

106   We hypothesized that: (i) The communities originating from locations with different

107   histories of hydrodynamic disturbance had different species compositions; that (ii) the origin

108   of the species communities from the natural gradient of hydrodynamic disturbance determine

109   their resilience to mechanical disturbance (historically higher levels of hydrodynamic stress

110   correlate with high resilience to experimental disturbance); and that (iii) dispersal, through

111   enabling patch-connectivity, mitigates negative impacts of disturbance in the

112   metacommunities.

113   **Material and methods**

114   *Study organisms and local conditions*

115   We collected benthic diatom communities from three sites on the mudflat off the coast

116   of Schiermonnikoog island, the Wadden Sea, in October of 2015, immediately before the start

117   of the experiment. The three sites were on a transect spanning from the coast seaward and

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118   crossing an intertidal mussel bed. Due to the crossing of the mussel bed, the sites differed in

119   exposure to hydrodynamic stress conditions and consequently sediment characteristics (Table

120   1). Site 1 was unprotected from hydrodynamic stress and in a sandy area coastward of the

121   mussel bed. Site 2 was seaward of the mussel bed with intermediate protection and muddy

122   sediment. Site 3 (hereafter referred to as "low hydrodynamic stress") was on a mussel bed,

123   where hydrodynamic stress was reduced and the sediment in the bare patches between

124   mussels was muddy and fine grained.

125   At each site, we collected the top 0.5 cm surface sediment of an area of 0.5 m^2 to

126   extract the benthic diatom communities to use in the experiment. Additionally, at each site we

127   took sediment cores (diameter: 26 mm) to measure chlorophyll a (three cores of 0.2 cm depth

128   pooled onto a piece of aluminum foil and stored in a sealed plastic bag on ice), organic matter

129   content at two different depths: 2 cm and 0.2 cm depth (i.e. shallow OM); placed into sealed

130   plastic bags and stored on ice), and benthic diatom species composition (core with 2 cm

131   depth; placed in sealed plastic bag and stored on ice). We also measured the level of

132   hydrodynamic disturbance at each site by placing dissolution plasters out for two tidal cycles

133   and measuring the dry weight of the plasters before and after exposure to the tides. We

134   transported all samples in cool boxes back to the laboratory (<24h).

135   In the laboratory, we extracted the motile benthic diatoms from the large area and from

136   the cores separately by spreading out the sediment and placing two layers of lens cleaning

137   tissue onto the sediment. After 5 h of exposure to light, we collected the top tissue and rinsed

138   the diatoms off into culture bottles with sterile filtered North Sea water. We stored the

139   samples from the large area in the dark at 19°C until the start of the experiment (<4h). We

140   fixed the core samples in Lugol's iodine and determined species composition with the

141   Utermöhl counting technique (Utermöhl 1958) under an inverted microscope. We freeze-dried

142   the sediment chlorophyll a samples, and subsequently measured chlorophyll a concentrations

143   using a fluorometer (Trilogy) after acetone extraction (90%, dark, -20°C, 48 h) and methods

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144   described by Jeffrey and Humphrey (1975). The organic matter content was determined

145   through Loss on Ignition by burning oven dried organic matter samples (48h, 60°C) in a

146   muffle kiln (4h, 550°C).

147   *Set-up and sampling*

148   We set up the experiment in a climate room with controlled temperature (19°C) and

149   light levels (10.8 µmol m^{-2} s^{-1} and 14:10 light-dark cycle). We used 60-mL-culture flasks

150   (TPP, filter screw cap) as microcosms for this experiment and 40 mL sterile filtered North Sea

151   water (N:Si:P added for final concentrations of 40:40:2.7 µM) as the medium. We carefully

152   exchanged 20 mL of the medium every third day over the course of the experiment to avoid

153   nutrient limitation.

154   For our fully factorial experiment, we constructed 54 metacommunities out of 162

155   local communities. We constructed the metacommunities by connecting three local

156   communities with different origin along the hydrodynamic stress gradient so that each

157   metacommunity contained one local community of high, medium, and low hydrodynamic

158   stress. We adjusted the inocula so that all bottles had similar initial diatom abundances. We

159   applied three different mechanical disturbance levels to the communities: no, intermediate,

160   and frequent. We administered disturbance by scraping the bottom of the culture flask with a

161   cell scraper every fourth day for intermediate and every other day for frequent disturbance

162   levels. The no-disturbance treatment was not subject to scraping. Each local community

163   within a metacommunity was subject to the same disturbance treatment. Half of the local

164   communities were assigned to a dispersal treatment, in which we administered dispersal every

165   other day. To administer dispersal, we first carefully turned the bottles three times to suspend

166   the more loosely attached diatoms into the medium. We then pipetted three mL solution (i.e.

167   medium plus suspended diatoms) out of each of the three bottles per metacommunity into a

168   sterile beaker. In the beaker, we mixed the three local community solutions and returned three

169   mL of this mixture into the respective bottles of the same metacommunity. The communities

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170   not subject to dispersal, were treated similarly to the dispersal treatment with the exception

171   that no culture was removed from or added to the bottles. This ensured that the dispersal

172   treatment did not affect boundary layer and nutrient uptake dynamics. The experiment ran for

173   29 days and we sampled destructively three times (i.e. removed the entire flask from the

174   experiment after two, three, and four weeks of growth). Each treatment combination

175   (including the three sampling times) was replicated three times.

176   On the three sampling days, we scraped the biofilm off the bottom of the culture flasks

177   and homogenized it in the medium by shaking the flask. We filtered 7 mL of the suspended

178   cultures over GF/F filters to determine chlorophyll *a* concentration of the samples. We

179   measured chlorophyll *a* concentration with a fluorimeter (Trilogy) after extraction with 90%

180   acetone. We calculated regional chlorophyll *a* concentration by summing the separate values

181   from each local community within a metacommunity.

182   *Statistical analysis*

183   Our fully crossed design included the fixed factors sampling day (three levels: 2, 3, 4),

184   origin (three levels: low hydrodynamic stress, medium hydrodynamic stress, and high

185   hydrodynamic stress), disturbance treatment (three levels: no, intermediate, frequent), and

186   dispersal treatment (two levels: no-dispersal and dispersal). We ran a GLM including all

187   factors and combinations to test the effect of sampling day, origin, disturbance, and dispersal

188   on local chlorophyll *a* concentration. Likewise, on the regional scale, we constructed a model

189   testing the effect of sampling day, disturbance, and dispersal on chlorophyll *a* concentration.

190   Subsequently, we compared treatment levels of the significant main effects (origin and

191   disturbance) with Tukey HSD post-hoc tests. All analysis were done in R v.3.4.1 (R Core

192   Team 2017).

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194   **Results**

195   *Local conditions at origin and initial species composition*

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196   As expected, the extraction sites of benthic diatoms varied in their characteristics

197   relating to hydrodynamic stress exposure and thus their sediment properties (Table 1). The

198   unprotected Site 1 (hereafter referred to as "high hydrodynamic stress") had the highest

199   erosion, but lowest organic matter content and chlorophyll *a* concentration (Table 1). Site 2

200   with intermediate protection (hereafter referred to as "medium hydrodynamic stress) had

201   intermediate erosion and organic matter content, but high chlorophyll *a* concentration (Table

202   1). The most protected Site 3 (hereafter referred to as "low hydrodynamic stress") had the

203   lowest erosion, but the highest organic matter content and chlorophyll *a* concentration (Table

204   1).

205   The different communities from different origin along the hydrodynamic stress

206   gradient also had varying benthic diatom species composition (Fig. 1). Site "high

207   hydrodynamic stress" was dominated by several larger *Navicula Sp.*, whereas Site "low

208   hydrodynamic stress" had a high relative abundance of the smallest *Navicula Sp* (Fig. 1). Site

209   "medium hydrodynamic stress" was dominated by *Pleurosigma aestuarii*, a very large

210   sigmoidal species (Fig. 1).

211   *Experimental results*

212   The origin of the diatom communities along the hydrodynamic stress gradient

213   determined the response of the communities to mechanical stress (significant interaction

214   effect between origin and mechanical disturbance: $F_{4,105}=8.54$, $p<0.01$; Fig. 2). Mechanical

215   disturbance significantly decreased local chlorophyll *a* concentrations in all communities

216   (significant main effect of disturbance: $F_{2,105}=45.63$, $p<0.01$) with both disturbance treatments

217   (i.e. intermediate (I) and frequent (F) mechanical disturbance) having significantly lower

218   chlorophyll *a* concentrations than the no-disturbance (N) treatment (Tukey HSD: N-I and N-F

219    $p<0.01$; Fig. 2). However, the higher hydrodynamic stress regime the communities originated

220   from, the more resilient they were to the mechanical disturbance treatment. On average, the

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221   mechanical disturbance decreased chlorophyll *a* in the communities with high hydrodynamic

222   stress at origin by 29%, with medium hydrodynamic stress at origin by 44%, and with low

223   hydrodynamic stress at origin by 74% (Tukey HSD origin: high-medium, high-low, and

224   medium-low p<0.01; Fig. 2).

225   Local chlorophyll a was also significantly affected by interactive effects of origin of

226   the community and dispersal ($F_{2,105}$=5.3, p=0.01). While dispersal decreased chlorophyll *a*

227   concentrations in the local communities originating from highest hydrodynamic stress, it did

228   not affect or slightly increased chlorophyll *a* concentrations in the other communities (origin

229   from medium and low hydrodynamic stress, respectively) (Fig. 2). There was no significant

230   effect of sampling day (Table A1).

231   Disturbance significantly decreased regional chlorophyll *a* concentration ($F_{2,35}$ =

232   21.08, p<0.01; N: 313.67±28.29; I: 186.52±13.60; F: 153.20±7.51; Tukey HSD: N-I and N-F

233   p<0.01; Fig. 2), while dispersal and sampling day did not have a significant effect on regional

234   chlorophyll *a* concentration (Fig. 2; Table A2).

235   **Discussion**

236   Our results demonstrate that the biological properties determined by the origin of the

237   experimental communities along a natural hydrodynamic stress gradient determined their

238   response to new disturbances. The communities with different histories of hydrodynamic

239   stress at origin had different species composition (supporting hypothesis 1). Communities

240   originating from sites that naturally experienced higher levels of hydrodynamic stress had a

241   higher resilience to experimental disturbance than those originating from sites with lower

242   levels of hydrodynamic disturbance (supporting hypothesis 2). However, dispersal did not

243   mitigate negative impacts of disturbance in our experimental metacommunities (rejecting

244   hypothesis 3). Thus, the different communities had different biological properties relating to

245   ecological memory (species composition, diversity, and traits); and the ecological memory of

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246   the communities shaped by higher levels of disturbance at origin were more resilient to new

247   disturbances than the communities with lower levels of disturbance at origin.

248   The variation in species composition at origin (Fig. 1) was likely caused by the differences

249   in local conditions on the intertidal flat including hydrodynamic stress and resulting sediment

250   characteristics (Table 1). Communities previously exposed to higher levels of hydrodynamic

251   stress are probably more resilient to novel disturbances because they are inhabited by species

252   that compensate the disturbance by individual resilience or by rapid growth rates due to

253   previous need for this. Changes in species composition as response to past states is part of the

254   ecological memory of communities. In our study, the ecological memory of the communities

255   originating from the site with high hydrodynamic stress likely contributed to mitigating the

256   negative impact of a novel disturbance on ecosystem functioning. Several other studies also

257   show that ecological memory increases the resilience of communities to novel disturbances in

258   different systems, including terrestrial plants (Johnstone et al. 2016), aquatic plants (Sterk et

259   al. 2016), corals (Hughes et al. 2019), and archaea (Beer et al. 2014). However, it is important

260   to realize that ecological memory is not a universal insurance for resilience, especially

261   considering the projected increase in magnitude and frequency of extreme climate events in

262   the future (Harley et al. 2006, IPCC 2014), which will make disturbance regimes more

263   unpredictable. For example, a recent study by Jacquet and Altermatt (2020) shows that above

264   a certain threshold of past disturbance frequency and intensity, legacy effects can lead to

265   negative effects of past disturbances on present species diversity and ecosystem functioning.

266   The positive effect of ecological memory also depends on species co-tolerance. Only when

267   species' initial tolerance and tolerance to additional stressors are positively correlated can the

268   impact of an additional stressor be reduced and lead to "stress-induced community tolerance"

269   (Vinebrooke et al. 2004). More research is needed to assess in which cases the positive effect

270   of ecological memory surpasses the negative effect of legacy effects and what other

271   components of ecological memory are important for community resilience.

272   Previous studies have shown that microalgal species composition and biomass

273   production are dependent on many abiotic and biotic variables and that they are tightly linked

274   to sediment grain size (Cahoon et al. 1999, Thornton et al. 2002, Du et al. 2009). Even though

275   we did not directly measure sediment grain size in this study, visual observations showed that

276   the sandy site with high hydrodynamic stress and low organic matter content had larger grain

277   size. Other studies confirm that locations with high hydrodynamic forcing have larger

278   sediment grain size and lower clay content and therefore are less muddy (de Jong & de Jonge

279   1995, Thornton et al. 2002, Méléder et al 2007). Smaller species should be able to recover

280   faster after disturbances, because they have higher growth and division rates (Finkel et al.

281   2010). Therefore, it would be logical to find that communities with smaller species can

282   withstand disturbances better, and thus in our study we would expect to find smaller species

283   in the more highly disturbed sites. We observed the opposite pattern. Species from the high

284   and medium stressed sites were generally larger than those from the low stressed site,

285   independent of sediment grain size at origin. Since in our study the finer grained sediments

286   were in the location of the mussel bed, it is unclear if the sediment determined diatom cell

287   size, or if other factors played into the size selection of species. For example, selective

288   grazing by organisms inhabiting the mussel bed could have influenced benthic diatom species

289   composition and thus possibly led to size discrimination and the presence of predominantly

290   small species in the fine-grained sediment (D'Hondt et al. 2018). In addition, diatoms are

291   generally characterized by high growth rates and maximum nutrient uptake rates, because

292   they are adapted to rapidly responding to nutrient pulses in coastal areas (Litchman et al.

293   2007). Therefore, the metabolic size scaling might not express in this group of diatoms.

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294   Alternatively, this scaling might be masked by local adaptation to hydrodynamic stress in the

295   communities investigated here and thus overridden by ecological memory.

296   Contrary to expectations, dispersal did not lead to increased chlorophyll *a*

297   concentration on the local nor regional scale, independent of the disturbance level. In the

298   community originating from high stress hydrodynamic conditions, dispersal even decreased

299   chlorophyll *a* compared to the no-dispersal treatment (Fig. 2). Interestingly, the variability of

300   replicates within the dispersal treatment of the no-disturbance communities was high,

301   meaning that the response of these replicates was not uniform. Contrary to the present results,

302   other studies have shown that dispersal indeed "rescues" disturbed communities (Altermatt et

303   al. 2011, Symons & Arnott 2013, Rosset et al. 2017). Through dispersal, communities gain

304   access to a larger species pool on the regional scale so that there should be more species

305   present that have the ideal traits for the novel situation after a disturbance. However, in our

306   experiment, even the intermediate disturbance level seemed too severe, or the dispersal

307   frequency too low, to initiate a rescue effect. Another explanation for our results could be that

308   in our experiment all local communities in a disturbed metacommunity were exposed to the

309   same disturbance level (i.e. the disturbance was a regional event), whereas in nature and in

310   other experiments, the regional species pool oftentimes includes disturbed and undisturbed

311   patches (e.g. Altermatt et al. 2011) so that within the metacommunity dispersal from the

312   undisturbed to disturbed patches can lead to a "rescue effect". In future experiments,

313   including undisturbed "rescue" patches would be a useful addition to the experimental set-up.

314   Our experiment shows that initial community composition (specifically relating to

315   ecological memory) largely drives ecosystem functions, despite the presence of other well-

316   known structuring mechanisms, such as dispersal. This exemplifies the important role of

317   species identities for ecosystem functioning in (meta)communities and highlights the crucial

318   need for protecting biodiversity in natural systems.

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489   **Tables**

490   **Table 1.** Site characteristics of the sample origins. (Origin = hydrodynamic stress exposure at

491   origin, Sed. = sediment type). Erosion was measured with dissolution plasters and is used as a

492   proxy for hydrodynamic forcing. Organic matter content in the sediment was calculated for

493   two different depths: 2 cm (Organic Matter) and 0.2 cm (Shallow OM).

Site	Coordinates	Origin	Sed.	Erosion (%)	Chlorophyll *a* (µg/g)	Organic Matter (%)	Shallow OM (%)
1	N53.47090, E6.22400	High	Sand	5.10	21.77	0.70	1.00
2	N53.46686, E6.22469	Medium	Mud	3.33	259.03	2.48	11.74
3	N53.46776, E6.22462	Low	Mud	2.77	293.40	10.04	12.76

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496 **Table 2.** Abbreviations as used in Fig. 1, names, and average cell size of the most abundant
497 diatom species.

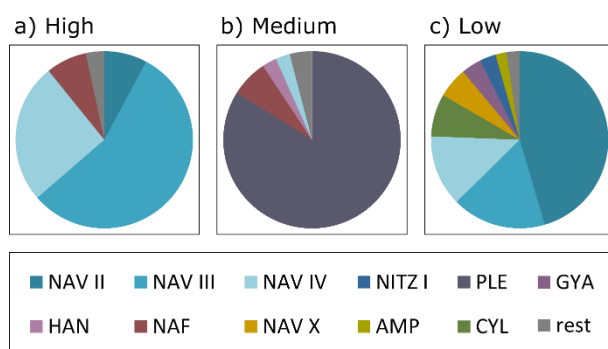| ID	Species	Cell size (μm^3)
AMP	*Amphora Sp. 1*	787.92
CYL	*Cylindrotheca closterium*	33.16
GYA	*Gyrosigma acuminatum*	1440.38
HAN	*Hantzschia Sp. 1*	612.90
NAF	*Navicula forcipata*	1563.89
NAV II	*Navicula Sp. 1*	49.74
NAV III	*Navicula Sp. 2*	146.92
NAV IV	*Navicula Sp. 3*	730.88
NAV X	*Navicula Sp. 4*	730.88
NITZ I	*Nitzschia Sp. 1*	193.73
PLE	*Pleurosigma aestuarii*	4783.61

498

499   **Figure Legends**

500   **Fig. 1.** Species composition at different extraction sites (origin). High, medium, and low refer

501   to hydrodynamic stress conditions at the origin (see Table 1). For names and average cell sizes

502   of the different species see Table 2.

503   **Fig. 2.** Chlorophyll *a* concentration in the different treatments for each local community with

504   different origin along a hydrodynamic stress gradient and for the regional scale. (a) High

505   hydrodynamic stress at origin, b) medium hydrodynamic stress at origin, c) low

506   hydrodynamic stress at origin, d) regional. Solid circles represent no-dispersal treatments and

507   open circles represent dispersal treatments. No (green), intermediate (orange), and frequent

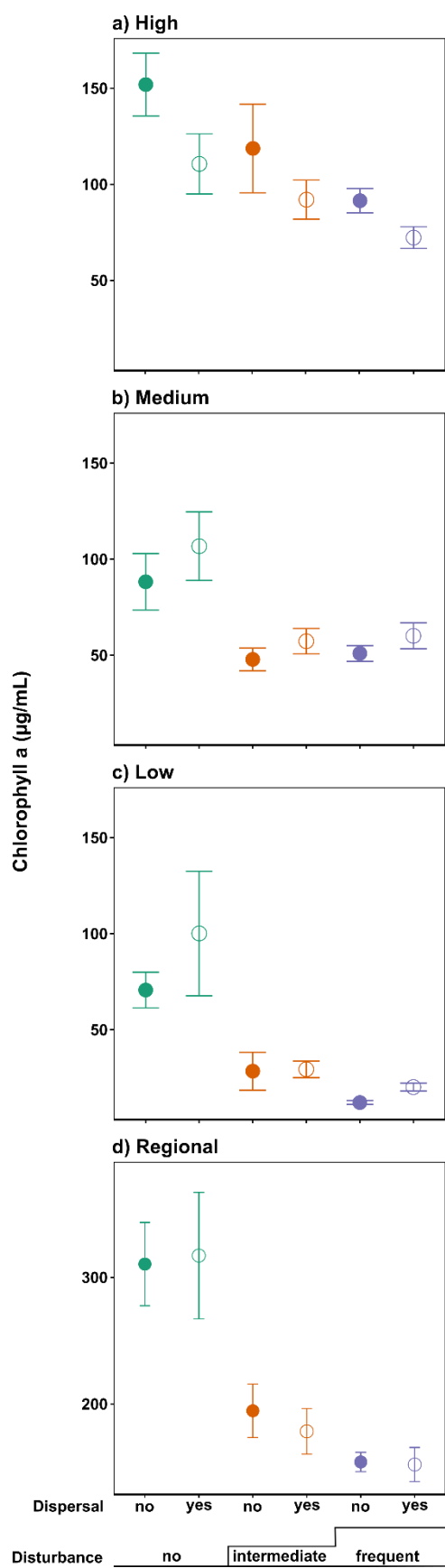508   (purple) correspond to the levels of the disturbance treatment in the experiment.

509   **Figures**

510

511   Fig. 1.

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513

514   Fig. 2.